Current available strategies to mitigate greenhouse gas emissions in livestock systems: an animal welfare perspective

Llonch, P; Haskell, MJ; Dewhurst, RJ; Turner, SP

Published in:
Animal

DOI:
10.1017/S1751731116001440

Print publication: 01/01/2017

Review: Current available strategies to mitigate greenhouse gas emissions in livestock systems: an animal welfare perspective

P. Llonch[1,a], M. J. Haskell[1], R. J. Dewhurst[2] and S. P. Turner[1]

[1]*Animal and Veterinary Sciences, Scotland's Rural College, West Mains Road, Edinburgh, EH9 3JG, United Kingdom*

[2]*Future Farming Systems, Scotland's Rural College, West Mains Road, Edinburgh, EH9 3JG, United Kingdom*

[a]*Present address: School of Veterinary Science, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain.*

Corresponding author: Pol Llonch. Email: pol.llonch@uab.cat

Short title

Welfare trade-offs with livestock GHG mitigation

Abstract

Livestock production is a major contributor to greenhouse gas (GHG) emissions, so will play a significant role in the mitigation effort. Recent literature highlights different strategies to mitigate GHG emissions in the livestock sector. Animal welfare is a criterion of sustainability and any strategy designed to reduce the carbon footprint of livestock production should consider animal welfare amongst other sustainability metrics. We discuss and tabulate the likely relationships and trade-offs between the

GHG mitigation potential of mitigation strategies and their welfare consequences, focusing on ruminant species and on cattle in particular. The major livestock GHG mitigation strategies were classified according to their mitigation approach as reducing total emissions (inhibiting methane production in the rumen), or reducing emissions intensity (Ei; reducing CH_4 per output unit without directly targeting methanogenesis). Strategies classified as antimethanogenic included chemical inhibitors, electron acceptors (i.e. nitrates), Ionophores (i.e. Monensin) and dietary lipids. Increasing diet digestibility, intensive housing, improving health and welfare, increasing reproductive efficiency and breeding for higher productivity were categorised as strategies that reduce Ei. Strategies that increase productivity are very promising ways to reduce the livestock carbon footprint, though in intensive systems this is likely to be achieved at the cost of welfare. Other strategies can effectively reduce GHG emissions whilst simultaneously improving animal welfare (e.g. feed supplementation or improving health). These win-win strategies should be strongly supported as they address both environmental and ethical sustainability. In order to identify the most cost-effective measures for improving environmental sustainability of livestock production, the consequences of current and future strategies for animal welfare must be scrutinized and contrasted against their effectiveness in mitigating climate change.

Keywords

Animal welfare, Climate change, Livestock, Mitigation, Sustainability

Implications

Livestock is a major contributor to climate change. In the context of an expected increase in the consumption of animal products, livestock producers must reduce their impact on the environment. A number of strategies have been proposed to reduce greenhouse gas emissions from livestock, including ruminants. These strategies are based on changes in feeding, breeding and management practices. However, their implications for the animal's health and welfare still need to be explored. This paper tabulates and discusses the potential welfare hazards and benefits of implementing the most prominent strategies and identifies the most cost-effective (GHG reduction *vs.* welfare) strategies to mitigate climate change.

Contribution of livestock to global greenhouse gas emissions

The global livestock sector contributes significantly to anthropogenic greenhouse gas (GHG) emissions. Direct emissions (through enteric fermentation and losses from manure) from livestock are estimated to contribute 11 percent of total anthropogenic GHG emissions (Gerber *et al*. 2013). Due to their greater total biomass than other livestock and their digestive strategy, ruminants are the most significant livestock producers of GHGs (Pitesky *et al*. 2009). Beef and dairy production account for the majority of emissions, contributing 41 and 20 percent respectively of the sector's direct emissions (FAO, 2013), much higher than pig and poultry which contribute 9 and 8 percent respectively

Enteric fermentation is considered a primary source of global anthropogenic methane (CH_4) emissions and in 2010 was estimated to be responsible for 30-40 percent of world-wide livestock emissions (CO_2-eq/year) followed by nitrous oxide (N_2O) (between 17-27 %) (Weiss and Leip, 2012; Tubiello *et al*., 2013). N_2O comes from transformations within management and deposition of animal (ruminants and monogastrics) manures on pastures (O'Mara, 2011). The highest percentage of livestock N_2O emissions are derived from cattle (60%), followed by monogastrics (21.6%) and small ruminants (18.8%) (Zervas and Tsiplakou, 2012). The severity of the environmental problem is expected to increase as a result of growth of the world population and demand for food. Popp *et al*. (2010) estimated that agricultural non-CO_2 emissions (CH_4 and N_2O) will triple by 2055, if no mitigation strategies are implemented, due to increased demand for animal products. Estimates from Smith et al. (2007) for 2020 project a 30 percent growth of CH_4 emissions. Besides the environmental concerns, enteric CH_4 production negatively affects energy efficiency in ruminants. For instance, up to 11% of gross energy in cattle feed can be lost via eructated CH_4 (Moraes et al., 2012). Therefore, emission mitigation can drive an improvement in production efficiency and economic returns for producers.

Animal welfare has been defined in several ways and using numerous criteria (e.g. biological function, behavioural ecology or emotional state). There is one approach that gathers all these aspects to an apparently simple definition of animal welfare; animals are healthy and they have what they want (Dawkins, 2006). This definition stresses the importance of good health and animal needs (either physical or emotional) to achieve good standards of welfare. Animal welfare is considered to be a necessary element of sustainable animal production (Broom, 2010). Increasingly, society demands that animal welfare be integrated into the concept of sustainable livestock production

(Appleby, 2005). A growing number of consumers demand ethical production systems and refuse to buy products if they are produced under morally unacceptable circumstances (Broom et al., 2013). For example, Clonan et al. (2015) found that welfare is a choice criterion for 88% of surveyed consumers when buying any meat. In the context of climate change mitigation, animal welfare should therefore be maximised, or at least protected from deterioration, when implementing any mitigation strategy.

Some of the husbandry strategies to reduce the carbon footprint of livestock production have already been proven effective under experimental or commercial conditions. Mitigation of GHG emissions in low input production systems, where there is still much room for nutritional and genetic improvement, can probably be achieved with minimal intensification, reducing emissions intensity (Ei) and improving animal welfare at the same time. But in modern high input livestock systems, the implementation of mitigation measures is likely to be at the cost of animal welfare. However, in many situations there is little information about the potential implications of adopting mitigation measures on the health and welfare of animals. The aims of this review are to identify the potential consequences, either positive or negative, for welfare of implementing strategies with proven efficacy to reduce GHG emissions from livestock, with a particular focus on ruminants, and to classify these strategies according to how they trade-off animal welfare and mitigation effectiveness.

Strategies for greenhouse gas mitigation and their implications for animal welfare

Strategies to mitigate enteric CH_4 and manure N_2O emissions from livestock production have recently been reviewed (Eckard *et al*., 2010; Gill *et al*., 2010; Buddle *et al*., 2011;

Zervas and Tsiplakou, 2012; Bellarby *et al*. 2013; Gerber *et al*., 2013; Hristov *et al*., 2013a,b). Among these, some strategies focus on reducing the indirect GHG produced during animal production such as, for example, land use change, direct on-farm energy use for livestock production or manure management. Another group of strategies focus on direct emissions from livestock such as CH_4 from enteric fermentation. Although indirect mitigation options that reduce GHG emission associated with animal production are of great relevance, these will not be discussed in this review but rather we will focus on direct mitigation strategies. Generally, the main direct strategies to mitigate GHG emissions can be classified as either reducing rumen methanogenesis (Hristov *et al*. 2013a), which can be addressed either as reducing total emissions, or reducing emissions intensity (Ei) without directly targeting methanogenesis (relative GHG mitigation) (Hristov *et al*. 2013b). Strategies to reduce methanogenesis include supplementing with antimethanogenic agents (e.g. antibiotics reducing methanogen populations) or supplementing with electron (H^+) acceptors (e.g. nitrate salts). Although proven to be effective in reducing CH_4 emissions, these strategies disrupt the natural rumen function and their misuse could lead to rumen disorders (defined below) and potential health and other welfare problems. The second group of strategies are intended for both ruminants and monogastrics, and are based on increasing production efficiency in order to reduce GHG emissions while maintaining the level of production. Notable strategies from this group include increasing feed efficiency or improving the health status of the herd, which act as win-win strategies improving at the same time the environmental sustainability and either economic return or animal welfare respectively.

The most relevant strategies (Table 1), in terms of GHG mitigation efficacy, are classified below according to their mode of action and mitigation potential. Hazards and potential benefits of each mitigation strategy are discussed below in order to identify the strategies that are most likely to impact animal welfare or, conversely, the ones offering a dual benefit for the environment and animal welfare.

Anti-methanogenic strategies

Ruminants emit CH_4 as part of their digestive processes, which involves microbial fermentation (Jungbluth *et al*., 2001). The process of synthesizing CH_4 is performed by highly specialized methanogens (archaea) in order to utilise hydrogen (H_2) produced during fermentation (Hook *et al*., 2010). To a far lesser extent, monogastrics also produce CH_4 emissions - in this case as a result of fermentation of fibrous material in the hind-gut. There are also CH_4 emissions from manure, with the amount emitted greatly dependent on the way the manure is managed (Zervas and Tsiplakou, 2012).

In ruminants, CH_4 production is considered an efficiency loss. Strategies that achieve a reduction in CH_4 emissions may also benefit energy efficiency. This can be key, both for production and animal welfare, when energy availability is lower than energy needs (e.g. in peak lactation of high producing dairy cows) preventing metabolic diseases derived from negative energy balance (NEB).

A variety of dietary supplements, targeted towards ruminants, can help to reduce enteric CH_4 production. Chemical inhibitors, nitrate and ionophores, and the inclusion of lipids have been suggested for diet supplementation because of their proven ability to reduce CH_4 emissions and, in many cases, improve production efficiency. However, these compounds can have deleterious effects on health, ruminal function or metabolism. For instance, rumen fermentation might be impaired if disrupting methanogenesis leads to an accumulation of H_2 in the rumen. Hence, further knowledge on their health side effects is needed before widespread application. If they are to be used, it will be crucial to understand inclusion levels (according to weight, nutritional status and stage of production) and to adopt strategies to introduce them into diets gradually.

Chemical inhibitors. Among the most well described methanogenic inhibitors are bromochloromethane (BCM), 2-bromo-ethane sulfonate (BES) (Mitsumori *et al*., 2011) and chloroform (Knight *et al*., 2011). These agents can achieve large reductions (from 25 to 95%) in direct CH_4 production according to *in vivo* studies with sheep, goats and cattle (Hristov *et al*., 2013a; Martinez-Fernandez *et al*., 2013). This potential however, must be contrasted with the risk to human health (when animal-derived products are consumed) and to the environment (they are themselves potent GHGs), which makes their addition to farm animal diets unlikely. Besides the environmental and public health concerns, halogenated compounds may also threaten animal health. For example, studies with rodents confirmed that halomethanes (i.e. BCM and chloroform) are toxic to the liver and kidney both after single doses (Ilett *et al*., 1973; Smith *et al*., 1983) and continued exposure (14 days) (Condie *et al*. (1983). Also in rodent bioassays, Dunnick *et al*., (1987) reported an increased incidence of adenocarcinomas in the kidney, liver and large intestine after oral administration of BCM. A higher risk of cancer was also described after long-term chloroform exposure in humans (Reitz *et al*., 1990). The risk of toxicity using supplementation of halomethanes to reduce CH_4 emissions in ruminants has been reported by Patra (2012) with effects ranging from liver damage to death after a long period of diet supplementation. Considering all the detrimental side effects of halogenated compounds it is very unlikely that they could be used as routine supplements for CH_4 mitigation.

Recent research has identified alternative chemical compounds capable of inhibiting methanogenesis but, in contrast to halomethanes, without health side effects. The most effective one at present is 3-nitrooxypropanol (3NP) which has achieved a 24% reduction in CH_4 emissions in *in vivo* trials with sheep (Martinez-Fernandez *et al*., 2013) but more pronounced reductions in cattle (7 to 60%) (Haisan *et al*., 2014; Reynolds *et al*., 2014). Experiments that have tested 3NP have not reported health side effects attributable to its administration over 3-5 weeks. A more recent study (Hristov *et al*., 2015) extended the trial to 14 weeks, achieving an average 30% CH_4 reduction, and no toxic effects were observed. The 3NP compound is anticipated to be an effective and harmless dietary strategy to mitigate CH_4, however, more toxicity focused studies are warranted to confirm this before it is used on a commercial scale.

Electron acceptors (nitrates). Methane is synthesised in the rumen by archaea from H_2, produced during fermentation, and CO_2. Nitrates can replace CO_2 as an electron acceptor, forming ammonia, instead of CH_4, as an alternative H_2 sink in the rumen (McAllister and Newbold, 2008). Recent research with sheep (Nolan *et al*., 2010; van Zijderveld *et al*., 2010) and cattle (van Zijderveld *et al*., 2011; Hulshof *et al*., 2012) has shown promising results with nitrate supplementation, indicating reductions in enteric CH_4 production, of up to 50%, especially when supplementing forage based diets (Troy *et al.*, 2015). However, nitrate must be supplemented with caution as it can be toxic above certain doses leading to methaemoglobinaemia and carcinogenesis (Sinderal and Milkowski, 2012). The reviews by Bruning-Fann and Kaneene (1993) and more recently by Lee and Beauchemin (2014) and Yang *et al*. (2016) discuss in detail nitrate's role in metabolism, animal production, enteric CH_4 emissions and toxicity and how it may be safely used in practice.

Nitrite is formed in the rumen as an intermediate in the reduction of nitrate to ammonia. In the unadapted rumen, the rate of nitrate reduction is greater than nitrite reduction, leading to accumulation of nitrite in the rumen and subsequent absorption. In the blood, nitrite has a high affinity for haemoglobin (oxyHb) and forms methaemoglobin (metHb) which is incapable of oxygen transport (Mensinga *et al*., 2003; Ozmen *et al*., 2005). High levels of metHb (>50%), result in signs of poisoning characterised by depressed feed intake and production, absence of weight gain, immune suppression, respiratory distress, cyanosis, and even death (Bruning-Fann and Kaneene, 1993). Death can occur within 3 h of feeding when cows consume between 0.22-0.33 g nitrate/kg body weight (Burrows *et al*., 1987; Bruning-Fann and Kaneene, 1993). However, adapting animals progressively to a diet with nitrate enables the population of nitrite-reducing bacteria to grow, increasing the capacity to reduce nitrite (Allison and Reddy, 1984). In several experiments that tested nitrate supplementation to reduce CH_4 emissions, no clinical signs or methaemoglobinaemia were observed (Al-aboudi and Jones, 1985; Nolan *et al*., 2010) even when in some cases the concentration of metHb was 4 to 5 fold greater than the average levels in control animals (van Zijderveld *et al*., 2010). Nevertheless, it is anticipated that any potential overdose during routine nitrate supplementation could have severe implications for the health of the animal. In addition, the use of nitrates results in higher excretion of ammonia, if rations are not correctly formulated which also has negative environmental implications as it contaminates soils and water. So, the potential gains for environmental sustainability achieved by GHG mitigation would be partially countered by ammonia pollution.

Ionophores. Antibiotic ionophores, of which Monensin is the most routinely used, have been reported to reduce CH_4 emissions in ruminants (Eckard *et al*. 2010; Gill *et al*. 2010; Martin *et al*., 2010 and Grainger and Beauchemin, 2011). In beef cattle, Guan *et al*. (2006) found a 27 to 30% reduction of enteric CH_4 for two to four weeks but showed decreasing efficacy thereafter due to adaptation of the ruminal microflora to monensin. This effect declines to an 8-9% reduction in CH_4 when used in dairy cattle (Appuhamy *et al*., 2013). Ionophores also have the capacity to increase feed efficiency, decreasing the quantity of feed intake required to maintain productivity, and thus decrease CH_4 emissions per unit of product. Ionophores alter the microbial ecology of the intestine and result in increased carbon and nitrogen retention by the animal (Russell and Strobel, 1989). Monensin can improve feed efficiency in beef cattle on feedlots by 7.5% (Goodrich *et al*., 1984), on pasture by 15% (Potter *et al*., 1986), and for dairy cows by 2.5% (Duffield *et al*. 2008).

Since January 2006, the routine use of ionophores, principally for their growth promoting properties, has been banned in the European Union to control antibiotic resistance, preventing their use as a mitigation strategy in any of the 28 member states of the EU. However, ionophores are currently still used outside of the EU and therefore are still a valuable strategy for use in many other countries around the world.

In addition to helping to mitigate CH_4 emissions, ionophores also benefit animal health by several means. Monensin reduces morbidity and mortality among feedlot animals by decreasing the incidence of sub-clinical ruminal acidosis (SARA), bloat and bovine emphysema (Galyean and Owens, 1988; McGuffey *et al*. 2001). The incidence of acidosis is reduced by inhibition of the major microbial strains that contribute to lactic acid production such as Gram positive bacteria and ciliate protozoa (Dennis *et al*. 1981; Russell and Strobel, 1989). The anti-bloat effects of monensin are mediated by a direct inhibition of encapsulated ("slime-producing") bacteria, as well as a decrease in overall ruminal gas production (Galyean and Owens, 1988). Monensin prevents the bovine emphysema which results from inhalation of skatole produced by rumen lactobacilli (Honeyfield, *et al*., 1985).

Monensin also has the capacity to ameliorate negative energy balance during periods of high energy demand (e.g. early lactation in dairy cows) by enhancing digestibility (discussed in the next section) and reducing the mobilization of body fat (McGuffey *et al*., 2001). There are numerous studies that demonstrate a decrease in incidence of postpartum subclinical ketosis (Jonker *et al*., 1998; Duffield *et al*., 1999 and Green *et al*., 1999) in herds supplemented with monensin.

Contrasting with these multiple benefits, ionophores can be toxic in a single dose of 22 mg/kg BW or more, leading to death in three out of five adult cattle tested (Potter *et al*. 1984). The same authors tested the effects of continuous doses of monensin over seven days from 400 to 4000 mg/animal/day and found a reduction in feed intake to the point of anorexia (400-1000 mg/day), diarrhoea, depression, rapid breathing, ataxia (2000 mg/day) and death (4 out of 6 at a 2000mg/day and 5 out of 7 at a 4000 mg/day dose). The dosage of monensin required to reduce direct CH_4 emissions are approximately 32-36 mg/kg BW in beef cattle and 21 mg/kg BW in dairy cattle (Guan *et al*., 2006; Appuhamy *et al*., 2013), whereas for increasing feed efficiency the required dosage can range from 10 to 40 mg/kg of DM (Sauer *et al*., 1989; McGuffey *et al*., 2001; Guan *et al*., 2006; Martineau *et al*., 2007). Considering a range of DMI for cattle of between 10 and 20 kg/day, animals would be offered between 100 (for the lowest dose and intake) and 800 mg/day (for the highest dose and intake) either to improve feed efficiency or to reduce CH_4 emissions. According to previous work (i.e. Potter *et al*., 1984), if this quantity is supplemented continuously (more than 7 days) this could be toxic to cattle, whereas other literature established that this range is below the risk threshold (van Zijderveld *et al*., 2011). These contrasting results suggest that further investigation to define the appropriate dosage and method of administration to prevent ionophore toxicity in cattle is warranted. This lack of knowledge is even more evident in other ruminant species, such as sheep or goats.

Dietary lipids. Medium-chain fatty acids (FAs) are known to reduce methanogenesis by several mechanisms. The main ones are a) reducing the proportion of energy supply from fermentable carbohydrates, b) changing the rumen microbial population, particularly inhibiting rumen methanogens and, to a limited extent, c) biohydrogenation of unsaturated FAs that works as an hydrogen acceptor (Eckard *et al*., 2010; Machmüller, 2006). The combination of these effects can lead to reductions in CH_4 production of between 3.8 and 5.4% per 1% addition in lipids (up to 6% lipid supplementation on a DM basis) (Beauchemin *et al*., 2008; Martin *et al*., 2010). However the direct anti-microbial (bacteria and protozoa) effect of lipids in the rumen (Hristov *et al*., 2013a) may provoke a dysbiosis of the microbial population which leads to an impairment of ruminal function. As a result, feed intake and the digestibility of non-lipid energy sources (Jenkins and Jenny, 1989) are decreased. For example, adding up to 10% fat into the diet can result in a decrease in fibre digestibility of about 50% (Jenkins, 1993), the effects of which may be less severe when digesting non-structural carbohydrates such as starch (Zinn, 1988). To avoid the adverse effects of lipids on rumen function and productivity in sheep and beef cattle, Hess *et al.* (2008) suggested that lipid supplementation should not exceed 3 to 4% of total DMI, especially in diets containing a high proportion of fibre. However, if lipid supplementation is used as a CH_4 mitigation strategy fat supplementation should reach a 5-8% of diet DM (Machmüller, 2006; Grainger and Beauchemin, 2011). Supplementation of higher quantities of lipids into the diet impacts gastrointestinal function in ruminants, which could affect their nutritional status, influencing not only their welfare but also their production efficiency.

On the other hand, if supplemented appropriately, fat can provide an extra energy input in some high energy-demand production phases, such as gestation or lactation in dairy cattle. In high producing dairy cows, supplementary fat may alleviate the NEB that occurs during early lactation and consequently improve fertility and milk yield (Grummer and Carroll, 1991; Staples *et al*., 1998). Also, addition of dietary fat soon after calving may reduce the risk of ketosis and steatosis before peak lactation (Grummer, 1993). If energy requirements are low, provision of lipids as a source of energy can lead to fat deposition that in some cases can impact the animal fitness (e.g. obesity and fatty liver) (Grummer, 1993).. . Indeed, if supplemented appropriately lipids can decrease CH_4 emissions and provide an extra source of energy which can be beneficial when energy requirements are higher than nutritional provision. The quantity of inclusion has to be limited (4 to 8% depending on sources) to avoid impacting nutrition in ruminants.

Strategies to decrease emission intensity

Emission intensity is a measure of the quantity of GHG emissions generated per unit of output. It is (negatively) associated to the productivity of the system, measured in terms of output per animal, or on a whole herd basis, and based on the fact that more efficient systems or processes create less waste (including GHGs) per unit of output (Gerber *et al.*, 2011). For example, increasing efficiency would require fewer animals and/or animals with shorter lifetimes to produce the same quantity of product. This reduces the quantity of inputs necessary for production and hence associated waste (FAO, 2013). This mitigation approach can reduce GHG emissions and increase profitability at the same time. Nevertheless, a drive for improved system efficiency has driven livestock intensification (e.g. concentrate diets, restricted grazing, breeding for higher productivity, etc.) which, when a certain threshold is exceeded, may impair animal welfare (e.g. increasing stocking density). This threshold is more likely to be achieved in intensive systems where animal productivity is often achieved at the cost of animal welfare. In contrast, in less developed production systems, increasing animal efficiency will be achieved by improving breeding, nutrition and/or health with no detrimental (and even potentially beneficial) effects for animal welfare.

Increasing diet digestibility. A promising approach for reducing relative CH_4 emissions per unit of output from livestock is by improving the nutrient use efficiency (Gerber *et al*., 2011). This can be achieved either by adding more digestible feed ingredients (e.g. non fermentable carbohydrates), or by increasing the efficiency with which animals use the feed (e.g. through physical, chemical or enzymatic pre-feeding treatments). These effects may be translated to effects on CH_4 emissions per unit of DM intake or per unit of product (Ei; Blaxter, 1989; Yeates et al., 2000). Diets containing a higher proportion of starch reduce rumen pH and favour the production of propionate rather than acetate in the rumen (McAllister and Newbold, 2008), leading to a reduction of net CH_4. On the other hand, improving diet quality (either with higher proportions of starch or improving digestibility with pre-feeding treatments) will improve feed efficiency (more kg of product with the same input), which results in a reduction in Ei. Considering these effects, Lovett *et al*. (2006) showed that when feeding of concentrates increased (from 338 to 1403 kg head yr^{-1}) in dairy cows, the emissions of GHGs were reduced by 9.5% (CH_4) and 16% (N_2O) respectively. According to Hales *et al*. (2012), CH_4 emissions were 17% lower per unit of DMI from steers fed corn processed by steam-flaking compared to dry-rolling which produced a larger particle size. Although these examples are in ruminants, highly digestible diets have also been proposed as a strategy to mitigate GHG emissions in non-ruminant species (Bakker, 1996; Monteny *et al*., 2006), as improving feed accessibility will result in a greater feed efficiency and therefore a reduction of Ei.

Whilst the use of diets containing higher levels of fermentable carbohydrates can drive productivity, CH_4 mitigation and profitability, there are limits to this approach, particularly because of potential negative health consequences of diets containing very high levels of fermentable carbohydrates. Significant effects on CH_4 emissions are often achieved using levels of starch that could impair rumen function. In ruminants, both a greater proportion of dietary fermentable carbohydrates and a reduction in feed particle size may increase the risk of acidosis in the rumen (Owens *et al*., 1998). When rapidly fermentable carbohydrate supply is increased (or the accessibility of carbohydrates enhanced), the supply of total volatile fatty acids (VFA) and the concentration of lactate in the rumen is increased. When lactate accumulates, it leads to a drop in rumen pH. The low rumen pH and high osmolality associated with rumen acidosis can damage the ruminal and intestinal wall, decrease blood pH, and cause dehydration (Owens *et al*., 1998). Clinical diagnosis of acidosis depends on measurements of ruminal or blood acidity, with ruminal pH of 5.2 and 5.6 as benchmarks for acute acidosis and SARA, respectively (Cooper and Klopfenstein, 1996). In addition to making carbohydrates more accessible, a reduction in particle size reduces chewing activity and saliva secretion in cattle. As saliva acts as a buffer against low pH, a reduction in chewing activity may aggravate the acidosis (Beauchemin *et al*., 2003). Acute acidosis occurs after an abrupt increase in consumption of readily fermented carbohydrates. Its common clinical signs are anorexia, ataxia and dehydration that, together, can be fatal (Owens *et al*., 1998). Less severe, but much more frequent and persistent, is SARA in which feed intake and performance may be suppressed. SARA is also associated with other health problems, such as inflammation (liver abscesses or laminitis) associated with pain (Plaizier *et al*., 2008) or bloat and displaced abomasum (Nocek, 1997; Enemark, 2008; De Vries *et al*., 2011). In beef cattle, the health problems associated with acidosis reduce productivity (e.g. requiring an older slaughter age to reach a given carcass conformation), thereby increasing Ei. This highlights some situations in which poorer welfare (that can be due to disease and pain; Fraser *et al*., 2013), may be related to increased GHG emissions intensity. The relationship between animal welfare, production efficiency and GHG mitigation is discussed later in this paper.

According to Sauvant and Giger-Riverdin (2009), a small to moderate change in the proportion of concentrate in ruminant diets is unlikely to affect enteric CH_4 emissions. Instead, marked improvements can be expected beyond a 35 to 40% inclusion of grain in the diet (Gerber *et al*., 2013). For instance, to achieve a decrease of 9.5% CH_4 in dairy cattle, Lovett *et al*. (2006) increased non-fibre carbohydrates more than four-fold (from 338 to 1403 kg/head/yr). Diets containing a high proportion of fermentable carbohydrates are common in intensive beef and dairy cattle production as they achieve high production rates. At such a level of starch inclusion, acidosis can be prevented with appropriate feeding management and husbandry practices (Enemark, 2008). However, some degree of SARA may be inevitable both in beef (Nagaraja and Lechtenberg, 2007) and dairy cattle (Kleen *et al*, 2003) when high proportions of starch are included in the diet. Considering the concentrate inclusion levels to achieve significant CH_4 mitigation, the implementation of such a strategy should be accompanied by dietary and management preventive measures to decrease the incidence of side effects to the minimum.

Housing and management. Greater intensification of animal housing and livestock management can also contribute to decreasing the relative GHG emissions at an individual level. Intensification can be defined as the increased use of external inputs and services to increase the system efficiency which is typically associated with lower GHG emissions intensity (Burney *et al*., 2010; Crosson *et al*., 2011). A reduction in the area per animal (increasing the stocking rate) or restricting access to pasture, are characteristic of intensive systems. In dairy cattle, an increase of 33% in stocking rate is associated with a 38% increase in milk/ha according to the DairyMod model (Johnson *et al*., 2008). Although an increase in stocking rate results in a direct increase in CH_4/ ha of 26%, it reduces CO_{2}-eq/L milk by 19%. For efficient GHG mitigation, a high stocking density must be matched by an increase in feed supply as increasing stocking density alone would be expected to result in decreased production and increased GHG emissions intensity per animal (Baudracco *et al*., 2010). In addition, if the stocking rate in grazed systems reaches a threshold (which will vary with the type of pasture ecosystem) the capacity of pastures to operate as a carbon sink may be exceeded (Soussana *et al*., 2004). The reduction in GHG emissions in intensive systems may be achieved from additional factors as well; improved diet digestibility of grain-based *vs.* forage diets, a smaller proportion of the dietary energy being used for maintenance when animals are confined (Peters *et al*., 2010) and the ability to capture excreta to restrict N_2O emissions.

Increased stocking rate may compromise welfare. Competition for resources may increase f stocking density is increased, resulting in more frequent agonistic interactions and greater social stress, especially in indoor systems (Vessier *et al*. 2008). For instance, high stocking rates increases aggression, injuries and stress responses in pregnant pigs (Barnett *et al*., 1992; Salak-Johnson *et al*., 2007) and can lead to a reduction in survival and productivity in caged hens (Adams and Craig, 1985; Bell *et al*., 2004). High population density results in increased aggressive behaviour in sheep (Mui and Ledin, 2007) and cattle (Kondo *et al*., 1989) leading to social stress. In ruminant outdoor systems, increased stocking density may increase the risk of parasitic diseases due to increased pathogen exposure (Taylor, 2012). Considering the 30-50% increase in stocking density needed to significantly decrease GHG emissions in ruminants (Pinares-Patino *et al*., 2007; Johnson *et al*. 2008), detrimental impacts on the health and non-health aspects of welfare of animals can be anticipated. Conversely, improvements in welfare, for example through reduced social stress, can directly contribute to greater feed intake in cattle (De Vries *et al*., 2004) and improved feed efficiency in pigs (Vermeer *et al*., 2014) thereby improving production rates and should also be considered as a measure to mitigate GHG emissions.

Grazing restriction can also reduce both N_2O and CH_4 emissions. DeRamus *et al*. (2003) demonstrated that restricted grazing resulted in more efficient conversion of forage into meat and milk, leading to a 22% reduction in annual projected CH_4 emissions per animal. De Klein *et al*. (2001) showed a 40 to 57% reduction in N_2O emissions from cattle when grazing was restricted to 3 h/day compared to free access.

However, restricting access to pasture may impact the health and welfare of animals. In dairy cattle restricted grazing requires cows to be confined in housing systems. Lameness is increased in confinement due to contact with slurry and the concussive effects of concrete (Cook *et al*., 2004; Haskell *et al*., 2006). Furthermore, cattle and sheep evolved as ‘‘grazers’’ and show a demand for access to pasture provided that their nutritional requirements are met (Legrand *et al*., 2009). Preventing access to pasture is therefore likely to thwart expression of a natural behaviour, for which there is a high motivation, and cause frustration (Rutter, 2010). Indeed, the definition of animal welfare given previously states that providing the opportunity to have what domestic animals want is key for good standards of welfare. Promoting animal welfare demands that we consider not just the prevention of ‘harms’ to animals, but also provision of opportunities to have positive experiences. Therefore, facilitating grazing in animals that show motivation for it seems necessary for optimal welfare.

Conversely, positive effects of restricted grazing for welfare should be mentioned. For example, the high nutritional requirements of high genetic merit dairy cows are more easily met in intensive systems. For these animals, unless nutritional requirements are met in grazing systems, hunger and poor body condition may compromise health and welfare and require animals to trade-off motivational priorities, such as eating and resting (Charlton *et al*., 2011). Additional benefits of indoor housing include provision of shelter in bad weather (heat, cold and wet), protection against predators and reduced exposure to parasites.

In order to optimise the balance between GHG mitigation and animal welfare goals, mixed systems combining indoor housing, in which the nutritional needs can be easily addressed, and access to pasture, should be promoted.

Improving health and welfare. Good standards of animal welfare cannot be achieved in conditions of poor health, as already discussed by Dawkins (2006) and Fraser *et al*. (2013). Poorer livestock health and fitness are associated with behavioural and metabolic changes such as reduced feed intake, a reduction in ability to digest food and increased energy requirements for maintenance (Collard *et al*., 2000; Bareille *et al*., 2003). This can lead to an increase in the involuntary culling rate that in turn raises GHG emissions intensity (FAO, 2013). Improvements in health may also reduce inefficiencies from product condemnation and poorer productivity of individual animals (Wall *et al*. 2010; de Boer *et al*., 2011). Taking the example of dairy cattle, both lameness (Warnick *et al*. 2001) and mastitis (Wilson *et al*., 1997) reduce milk output, increasing non-CO_2 GHG emissions per litre of milk produced.

Better health may reduce culling due to injury and disease, and is therefore very likely to extend the average productive life span of the herd. In dairy cattle, increased average longevity of animals in the herd has been suggested as a means to enhance animal productivity and reduce GHG emissions per kg product (Weiske *et al*., 2006; Bell *et al*. 2011). The mitigation potential of this measure ranges from 1% (Beauchemin *et al*., 2011) to nearly 13% (Weiske *et al*., 2006) if the reduction in replacement rate and the export of surplus heifers from the system as newborns are considered.

Extended longevity can be a requirement for and/or an indicator of welfare (Broom, 2007; FAWC, 2009; Yeates, 2009) but it is closely related to whether a life is worth living. Longevity has been used as an indicator of welfare since it indicates whether health and biological functioning are compromised to such an extent that the life span is affected, although it does not necessarily translate that a long life is a one worth living. From this perspective, what is acceptable can be interpreted more broadly than merely preventing physical or mental discomfort and includes the possibility for animals to flourish and live a natural life (Bruijnis *et al*. 2013). In general, an extended life span will enhance production efficiency of breeding animals such as dairy cattle and, at the same time, will improve animal welfare. The impact of this strategy to decrease emission intensity in species other than cattle (i.e. pigs and sheep) should be studied to quantify its effectiveness in other species.

Improved animal health through the prevention and control of disease and parasites is widely regarded as fundamental to animal welfare (OIE, 2012). Animal welfare however is determined by health but also non-health aspects such as comfort, absence of fear or the ability to perform natural behaviours. Improvements in non-health aspects of animal welfare have not yet been tested as a specific strategy to reduce GHG emissions. However, in some circumstances (e.g. lower environmental stress) better animal welfare can benefit productivity and thus GHG Ei (Place and Mitloehner, 2014). Significant improvements in welfare and productivity can probably be achieved through basic husbandry changes. For instance, increased stress provoked by negative handling can reduce milk and meat production in dairy (Rushen *et al*., 1999) and beef cattle (Hemsworth and Coleman, 2011). In laying hens, social stress induced by overcrowding of caged hens can lead to a reduction in survival and productivity (Adams and Craig, 1985; Bell *et al*., 2004). The growth rate of pigs subjected to thermal stress, restricted space allowance, or regrouping can be depressed by 10, 16, and 11%, respectively, but by 31% when subjected to all three stressors simultaneously (Hyun *et al*., 1998). Some strategies that aim to increase animal productivity can thwart animal welfare but at the same time, improvements in animal welfare may, in some cases, improve animal productivity (and economic performance) and reduce GHG Ei.

Increasing reproductive efficiency. Poor fertility means that more breeding animals are required in the herd to meet production targets and more replacements are required to maintain the herd size, which increases the Ei at a herd level. According to Garnsworthy (2004), CH_4 emissions could be decreased by 10–11% and ammonia (precursor of N_2O) emissions by about 9% by restoring average fertility rates in dairy cattle to those in 1995. The reduction in CH_4 and ammonia could be as high as 24% and 17% respectively if further feasible improvements in fertility were achieved. Nevertheless, increasing reproductive pressure on dams may increase the metabolic demands associated with pregnancy over the cow's lifetime. Parturition and lactation results in an abrupt shift in the metabolic demands from body reserves to rapid mobilization of lipid and protein stores in support of milk production which frequently leads to NEB (Grummer, 2007). Improved reproductive efficiency (e.g. by reducing the interval between parities or increasing the number of offspring per parity) may increase the likelihood of NEB with detrimental consequences for animal health such as an increased risk of metabolic diseases (e.g. clinical hypocalcaemia and ketosis), reduced immune function and a reduction in subsequent fertility (Roche *et al*., 2009).

Decreasing the age at first calving has also been proposed as a strategy to mitigate GHG emissions intensity. Farrié *et al*. (2008) showed that by reducing the age at first calving of heifers from three to two years in a Charolais beef herd, the live birth rate increased from 5% to 10%. According to Nguyen *et al*. (2013), decreased calving age seems a promising strategy to mitigate GHG emissions by an estimated 8 to 10%. Heifers younger than 24 months are still growing and the energy requirements implicit in gestation and basal maintenance have to be added to those from growth (Roche *et al*., 2009). Frequently, aggregate energy requirements cannot be met by nutritional inputs, leading to greater NEB and mobilization of body reserves and an excessive decrease in body condition (Berry *et al*., 2006; Roche *et al*., 2007). A poor nutritional status at the point of calving will lead to a high incidence of diseases associated with metabolic exhaustion such as ketosis (Gillund *et al*., 2001), milk fever (Roche and Berry, 2006), displaced abomasum (Cameron *et al*., 1997) and fatty liver (Drackley, 1999). In addition, this low nutritional status will impact reproduction rates (i.e. reduced ovulation rate, increased likelihood for pregnancy loss, increased calving to conception interval, etc.) (Walsh *et al*., 2011), therefore impairing the system efficiency which inevitably increases the system emission intensity. Again, this is an example of a situation in which improving animal welfare (through reduced reproductive pressure) may help to mitigate Ei.

Conversely, stress can impair reproduction and its mitigation can provide significant improvements in reproductive output. In mammalian species, stress (particularly heat stress) can have large effects on most aspects of reproductive function; either male or female gamete formation and function, embryonic development and foetal growth and development (Hansen, 2009). In dairy cows, stress can exacerbate the effects of NEB because of a reduction in appetite and an increase in energy use to meet the demands of the stress response (Shehab-El-Deen *et al*., 2010). Stress experienced during the early gestation period causes embryonic loss in cattle (Hansen and Block, 2004). It is likely then that the control of stressors during gestation or a reduction in stress sensitivity will improve conception rates and foetal development and hence, benefit productivity and GHG mitigation.

Reproductive output can also be increased by means of an increase in litter size or increase in the number of offspring weaned. Greater litter sizes could have a significant impact on welfare in certain species. For example, increased litter size can have a major effect on offspring mortality (Mellor and Stafford, 2004) associated with a higher risk of starvation and thermal stress for lambs (Dwyer, 2008) and pigs (Rutherford *et al*., 2013). Single or twin lambs are much less likely to die than triplets (Barlow *et al*., 1987). Similarly, piglets from litters of 16-19 are much more likely to die than litters of 8-9 (45 *vs.* 10-15%) (Blasco *et al*., 1995). Conversely, greater numbers of weaned offspring can also be achieved by improving survival after birth. Wall (2002) suggested that improvements in pre-, peri- and post-partum offspring survival through improving calving and maternal traits could mitigate GHG emissions. Beauchemin *et al*. (2011) described a hypothetical scenario in which a 5% improvement in calf survival rate from birth to weaning (from 85 to 90%) would decrease GHG emissions by up to 4%. The consequences of increasing survival rates for offspring welfare are obvious. In addition, the death of a newborn might cause anxiety or frustration to its mother when appropriate feedback in response to maternal care is not received, as already suggested in sheep (Dwyer, 2008).

In conclusion, excessive reproductive pressure may be detrimental for the health of the mother and progeny. Other strategies to increase reproductive efficiency (i.e. improving offspring survival) may benefit both animal productivity and their welfare. Hence, adequate feeding and management of pregnant livestock and the provision of a suitable birth environment and appropriate care and husbandry for neonates are important determinants not only for fertility and neonatal survival, but also for GHG mitigation.

Breeding for increased productivity. Breeding for more productive animals helps mitigate GHG emissions through the dilution of nutrient requirements for maintenance where a given level of production can be achieved with fewer animals (Van de Haar and St Pierre, 2006; Wall *et al*. 2010; Bell *et al*. 2011). However, as already described by Rauw *et al*. (1998) and Lawrence *et al.* (2004), selective breeding for higher productivity can harm animal health and welfare unless balanced by selection pressure placed on functional traits. Genetic selection for high production efficiency can impair normal biological functioning (Oltenacu, 2009; De Vries *et al*., 2011; Fraser *et al*., 2013) and lead to numerous unexpected consequences (Table 1). A high genetic potential for mobilizing body energy reserves for production can have deleterious effects on health and fertility (Bell *et al*., 2011), as shown by the association between high milk production and an increased incidence of fertility problems and metabolic disorders such as ketosis in dairy cattle (Walsh *et al*., 2011). Evidence of this trade-off are the undesirable genetic correlations between milk yield and ketosis, mastitis and lameness during lactation (r_g=0.26-0.65, r_g=0.15-0.68 and r_g=0.24-0.48; respectively) reviewed by Ingvartsen *et al*. (2003). The link between breeding for increased production and risk of poor health has also been described in monogastrics. Osteoporosis is widespread in genetically selected commercial laying hens because of excessive loss of bone calcium that is repartitioned to egg shells (Webster, 2004; Whitehead, 2004). Osteoporosis increases the risk of fractured bones in caged birds when they are handled or when hens fall during flight (Lay *et al*., 2011). Moderate to strong genetic correlations have been estimated in pigs between rapid growth, litter size and feed conversion efficiency on the one hand and increased osteochondrosis and leg weakness on the other (Huang *et al*., 1995; Kadarmideen *et al*., 2004).

Improved feed efficiency is a promising approach to mitigate GHG emissions and progress has already been made in this direction through breeding. Waghorn and Hegarty (2011) estimated that if feed efficiency were selected as the main animal breeding goal for ruminants, a valuable 15% reduction in CH_4 emissions could be achieved. Reductions in emissions and emissions intensity with improved feed efficiency should also apply to N_2O (Gerber *et al*., 2013), as more N efficient animal will retain more dietary N and therefore N excretion in faeces and urine will decrease. Nevertheless, risks for health and fertility traits have been identified in breeding for greater feed efficiency. For example, if body condition is not included in the prediction of feed efficiency, a decline in fertility could result from body energy reserves being allocated to production rather than reproduction (Pryce *et al*., 2014). Furthermore, Waasmuth *et al*. (2000) estimated undesirable genetic correlations (r_g) between a measure of feed efficiency (feed conversion ratio; FCR) in growing bulls and health traits in lactating animals (mastitis, r_g −0.79; ketosis, r_g −0.37).

Whilst the GHG mitigation potential of breeding for increased efficiency and productivity may be significant, past experience highlights the need for broader breeding goals to offset negative welfare consequences that in turn have economic and environmental costs (Lawrence *et al*., 2004). In this regard, recent literature suggests that non-productive traits such as welfare can be improved in association with productivity traits in dairy cattle (Gaddis *et al*., 2014), pigs (Rowland *et al*., 2012) and poultry (Kapell *et al*., 2012). Reduced welfare is not a necessary consequence of selective breeding per se, and indeed, if used appropriately, animal breeding may have the potential to enhance animal welfare (Jones and Hocking, 1999).

Conclusions

In recent years, animal science has focused on reducing the environmental impacts of production while enhancing efficiency or profitability of herds and flocks as the primary goals, relegating the welfare of individual animals to a secondary consideration (Mellor *et al*., 2009). However, consumer concern for animal welfare is increasing and it is gradually accepted as an integral component of sustainability. In this context, the implications of strategies to reduce the environmental impact of livestock production for animal welfare are important.

Strategies to reduce GHG emissions from livestock production have come into focus in order to meet the commitments of international treaties on GHG mitigation. The majority of these strategies aim to increase productivity (unit of product per animal), which in most cases cannot be achieved without good standards of animal welfare. In other cases, GHG mitigation is targeted towards manipulating the naturalness of the animals' environment, risking a reduction in their welfare. For example, strategies focused on changing housing conditions increase the risk of social stress or compromise the expression of natural behaviour, which can cause frustration. Breeding strategies that aim to change animal phenotypes to enhance productivity or efficiency may have wide-ranging implications for welfare unless these effects are measured and controlled.

Some dietary measures, such as supplementing ionophores, can effectively reduce GHG emissions without negatively affecting animal welfare, whilst others can even improve it. For example, strategies reducing direct CH_4 emissions will increase energy availability benefiting the energy balance which can be critical in high producing animals. In some cases, improvements in animal welfare may enhance animal productivity, which will provide better economic returns to farmers and the livestock sector as, for example, through decreased social stress, enhanced health status or improved offspring survival. These “win-win-win” strategies, enhancing sustainability with regards to societal, environmental and economic concerns of livestock production should be strongly supported by decision makers.

Beyond the general conclusions above, there is still a great lack of knowledge on the repercussions for animal welfare of the known (and emerging) strategies to reduce GHG emissions. The consequences that such strategies could have on animal welfare must not only be identified, but also quantified and contrasted. This will allow a realistic and informed debate on what strategies should or should not be adopted to improve the environmental sustainability of livestock production without compromising animal welfare.

Acknowledgements

The authors gratefully acknowledge JA Rooke and E Wall for their valuable contributions to this paper. P Llonch received support from a Marie Curie Intra-European Fellowship within the 7th European Community Framework Programme

(PIEF-GA-2012-331505). SRUC receives financial support from the Scottish Government Strategic Research Programme.

References

The list of references used older than 2011 is given in Supplementary Material S2.

Abecia L, Toral PG, Martín-García AI, Martínez G, Tomkins NW, Molina-Alcaide E, Newbold CJ Yaňez-Ruiz DR 2012. Effect of bromochloromethane on methane emission, rumen fermentation pattern, milk yield, and fatty acid profile in lactating dairy goats. Journal of Dairy Science 95, 2027-2036.

Appuhamy RN, Strathe AB, Jayasundara S, Wagner-Riddle C, Dijkstra J, France J and Kebreab E 2013. Anti-methanogenic effects of monensin in dairy and beef cattle: A meta-analysis. Journal of Dairy Science 96, 5161-5173.

Beauchemin KA, Janzen HH, Little SM, McAllister TA and McGinn SM 2011. Mitigation of greenhouse gas emissions from beef production in western Canada; Evaluation using farm-based life cycle assessment. Animal Feed Science and Technology 166, 663-677.

Bell MJ, Wall E, Simm G and Russell G 2011. Effects of genetic line and feeding system on methane emissions from dairy systems. Animal Feed Science and Technology 166, 699-707.

Bellarby J, Tirado R, Leip A, Weiss F, Lesschen JP and Smith P 2013. Livestock greenhouse gas emissions and mitigation potential in Europe. Global Change Biology 19, 3-18.

Broom DM, Galindo FA and Murgueitio E 2013. Sustainable, efficient livestock production with high biodiversity and good welfare for animals. Proceedings of the Royal Society B: Biological Sciences 280, 1771.

Bruijnis MRN, Meijboom FLB and Stassen EN 2013. Longevity as an animal welfare issue applied to the case of foot disorders in dairy cattle. Journal of Agricultural and Environmental Ethics 26, 191-205.

Buddle BM, Denis M, Attwood GT, Altermann E, Janssen PH, Ronimus RS, Pinares-Patiño CS, Muetzel S and Neil Wedlock D 2011. Strategies to reduce methane emissions from farmed ruminants grazing on pasture. The Veterinary Journal 188, 11-17.

Charlton GL, Rutter SM, East M and Sinclair LA 2011. Preference of dairy cows: Indoor cubicle housing with access to a total mixed ration vs. access to pasture. Applied Animal Behaviour Science 130, 1-9.

Clonan A, Wilson P, Swift JA, Leibovici DG and Holdsworth M 2015. Red and processed meat consumption and purchasing behaviours and attitudes: impacts for human health, animal welfare and environmental sustainability. Public Health Nutrition, 1-11.

Crosson P, Shalloo L, O'Brien D, Lanigan GJ, Foley PA, Boland TM and Kenny DA 2011. A review of whole farm systems models of greenhouse gas emissions from beef and dairy cattle production systems. Animal Feed Science and Technology 166, 29-45.

De Boer IJM, Cederberg C, Eady S, Gollnow S, Kristensen T, Macleod M, Meul M, Nemecek T Phong LT, Thoma G, van der Werf HMG, Williams AG and Zonderland-Thomassen MA 2011. Greenhouse gas mitigation in animal production: towards an integrated life cycle sustainability assessment. Current Opinion in Environmental Sustainability 3, 423-431.

De Vries M, Bokkers EAM, Dijkstra T, Van Schaik G, De Boer IJM 2011. Associations between variables of routine herd data and dairy cattle welfare. Journal of Dairy Science 94, 3213-3228.

Food and Agriculture Organisation (FAO) 2013 Mitigation of greenhouse gas emissions in livestock production. A review of technical options for non-CO_2 emissions. FAO, Rome, Italy.

Fraser D, Duncan IJ, Edwards SA, Grandin T, Gregory NG, Guyonnet V, Hemsworth PH, Huertas SM, Huzzey JM, Mellor DJ, Mench JA, Špinka M and Whay HR 2013. General Principles for the welfare of animals in production systems: The underlying science and its application. The Veterinary Journal 198, 19-27.

Gaddis KP, Cole JB, Clay JS and Maltecca C 2014. Genomic selection for producer-recorded health event data in US dairy cattle. Journal of Dairy Science 97, 3190-3199.

Gerber PJ, Vellinga T, Opio C and Steinfeld H 2011. Productivity gains and emissions intensity in dairy systems. Livestock Science 138, 100-108.

Gerber PJ, Hristov AN, Henderson B, Makkar H, Oh J, Lee C, Meinen R, Montes F, Ott T, Firkins J, Rotz A, Dell C, Adesogan AT, Yang WZ, Tricarico JM, Kebreab E, Waghorn G, Dijkstra J and Oosting S 2013. Technical options for the mitigation of direct methane and nitrous oxide emissions from livestock: a review. Animal 7, 220-234.

Grainger C and Beauchemin KA 2011. Can enteric methane emissions from ruminants be lowered without lowering their production? Animal Feed Science and Technology 166-167, 308-320.

Haisan J, Sun Y, Guan LL, Beauchemin KA, Iwaasa A, Duval S, Barreda DR and Oba M 2014. The effects of feeding 3-nitrooxypropanol on methane emissions and productivity of Holstein cows in mid lactation. Journal of Dairy Science 97, 3110-3119.

Hales KE, Cole NA and MacDonald JC 2012. Effects of corn processing method and dietary inclusion of wet distillers grains with solubles on energy metabolism, carbon-nitrogen balance, and methane emissions of cattle. Journal of Animal Science 90, 3174–3185.

Hemsworth PH and Coleman GJ 2011 Human–Livestock Interactions In: The Stockperson and the Productivity and Welfare of Farmed Animals (Hemsworth PH and Coleman GJ Ed.) p 208. CABI, Wallingford, UK.

Hristov AN, Oh J, Firkins JL, Dijkstra J, Kebreab E, Waghorn G, Makkar HPS, Adesogan AT, Yang W, Lee C, Gerber PJ, Henderson B and Tricarico JM 2013. Mitigation of methane and nitrous oxide emissions from animal operations: I. A review of enteric methane mitigation options. Journal of Animal Science 91, 5045-5069.

Hristov AN, Ott T, Tricarico J, Rotz A, Waghorn G, Adesogan A, Dijkstra J, Montes FR, Oh J, Kebreab E, Oosting SJ, Gerber PJ, Henderson B, Makkar HP and Firkins JL 2013. Mitigation of methane and nitrous oxide emissions from animal operations: III. A review of animal management mitigation options. Journal of Animal Science 91, 5095-5113.

Hristov AN, Oh J, Giallongo F, Frederick TW, Harper MT, Weeks HL, Branco AF, Moate PJ, Deighton MH, Williams SRO, Kindermann M and Duval S 2015. An inhibitor persistently decreased enteric methane emission from dairy cows with no negative effect on milk production. Proceedings of the National Academy of Sciences, 112, 10663-10668.

Hulshof RBA, Berndt A, Gerrits WJJ, Dijkstra J, Van Zijderveld SM, Newbold JR and Perdok HB 2012. Dietary nitrate supplementation reduces methane emission in beef cattle fed sugarcane-based diets. Journal of Animal Science 90, 2317-2323.

International Panel of Climate Change (IPCC) 2013. Chapter 11 Agriculture, Forestry and Other Land Use (AFOLU). In: Climate Change 2014: Mitigation of Climate Change. IPCC Working Group III Contribution to AR5, Mitigation of Climate Change. Available at: http://report.mitigation2014.org/drafts/...r5_final-draft_postplenary_chapter11.pdf. Accessed at 28 November 2014.

Kapell DNRG, Hill WG, Neeteson AM, McAdam J, Koerhuis ANM and Avendaño S 2012. Twenty-five years of selection for improved leg health in purebred broiler lines and underlying genetic parameters. Poultry Science 91, 3032-3043.

Knight T, Ronimus RS, Dey D, Tootill C, Naylor G, Evans P, Molano G, Smith A, Tavendale M, Pinares-Patino CS and Clark H 2011. Chloroform decreases rumen methanogenesis and methanogen populations without altering rumen function in cattle. Animal Feed Science and Technololy 166, 101-112.

Lay DC, Fulton RM, Hester PY, Karcher DM, Kjaer JB, Mench JA, Mullens BA, Newberry RC, Nicol CJ, O'Sullivan NP and Porter RE 2011. Hen welfare in different housing systems. Poultry Science 90, 278-294.

Lee C and Beauchemin KA 2014. A review of feeding supplementary nitrate to ruminant animals: nitrate toxicity, methane emissions, and production performance. Canadian Journal of Animal Science 94, 557-570.

Martinez-Fernandez G, Arco A, Abecia L, Cantalapiedra-Hijar G, Molina-Alcaide E, Martin-Garcia AI, Kindermann M, Duval S and Yanez-Ruiz DR 2013. The addition of ethyl-3-nitrooxy propionate and 3-nitrooxypropanol in the diet of sheep sustainably reduces methane emissions and the effect persists over a month. Advances in Animal Biosciences 4, 368.

Mitsumori M, Shinkai T, Takenaka A, Enishi O, Higuchi K, Kobayashi Y, Nonaka I, Asanuma N, Denman SE and McSweeney CS 2011. Responses in digestion, rumen fermentation and microbial populations to inhibition of methane formation by a halogenated methane analogue. British Journal of Nutrition 8, 1-10.

Moraes LE, Strathe AB, Fadel JG, Casper DP and Kebreab E 2014. Prediction of enteric methane emissions from cattle. Global Change Biology 20, 2140-2148.

Nguyen TTH, Doreau M, Corson MS, Eugène M, Delaby L, Chesneau G, Gallard Y and Van der Werf HMG 2013. Effect of dairy production system, breed and co-product handling methods on environmental impacts at farm level. Journal of Environmental Management 120, 127-137.

Organization International des Epizooties (OIE) 2012. Introduction to the recommendations for animal welfare. In: Terrestrial Animal Health Code, 21st Ed. Article 7.1.4. World Organisation for Animal Health (OIE), Paris, France.

Patra AK 2012. Enteric methane mitigation technologies for ruminant livestock: a synthesis of current research and future directions. Environmental Monitoring and Assessment 184, 1929-1952.

Place SE and Mitloehner FM 2014. The nexus of environmental quality and livestock welfare. Annual Review Animal Biosciences 2, 555-569.

Pryce JE, Wales WJ, De Haas Y, Veerkamp RF and Hayes BJ 2014. Genomic selection for feed efficiency in dairy cattle. Animal 8, 1-10.

Reynolds CK, Humphries DJ, Kirton P, Kindermann M, Duval S and Steinberg W 2014. Effects of 3-nitrooxypropanol on methane emission, digestion, and energy and nitrogen balance of lactating dairy cows. Journal of Dairy Science 97, 3777-3789.

Rowland RR Lunney J and Dekkers J 2012. Control of porcine reproductive and respiratory syndrome (PRRS) through genetic improvements in disease resistance and tolerance. Frontiers in Genetics 3, 260.

Rutherford KMD, Baxter EM, D'Eath RB, Turner SP, Arnott G, Roehe R, B Ask, Sandøe P, Moustsen VA, Thorup F, Edwards SA, Berg, P and Lawrence AB 2013. The welfare implications of large litter size in the domestic pig I: biological factors. Animal Welfare 22, 199-218.

Sinderal JJ and Milkowski AL 2012. Human safety controversies surrounding nitrate and nitrite in the diet. Nitric Oxide 26, 259-266.

Taylor MA 2012. Emerging parasitic diseases of sheep. Veterinary Parasitology 189, 2-7.

Troy SM, Duthie CA, Hyslop JJ, Roehe R, Ross DW, Wallace RJ, Waterhouse A and Rooke JA 2015. Effectiveness of nitrate addition and increased oil content as methane mitigation strategies for beef cattle fed two contrasting basal diets. Journal of Animal Science 93, 1815-1823.

Tubiello FN, Salvatore M, Rossi S, Ferrara A, Fitton N and Smith P 2013. The FAOSTAT database of greenhouse gas emissions from agriculture. Environmental Research Letters 8, 015009.

Van Zijderveld SM, Gerrits WJJ, Dijkstra J, Newbold JR, Hulshof RBA and Perdok HB 2011. Persistency of methane mitigation by dietary nitrate supplementation in dairy cows. Journal of Dairy Science 94, 4028-4038.

Vermeer HM, de Greef KH, Houwers HWJ 2014. Space allowance and pen size affect welfare indicators and performance of growing pigs under Comfort Class conditions. Livestock Science 159, 79–86.

Waghorn GC and Hegarty RS 2011. Lowering ruminant methane emissions through improved feed conversion efficiency. Animal Feed Science and Technology 166, 291-301.

Walsh SW, Williams EJ and Evans ACO 2011. A review of the causes of poor fertility in high milk producing dairy cows. Animal Reproduction Science 123, 127-138.

Weiss F and Leip A 2012. Greenhouse gas emissions from the EU livestock sector: a life cycle assessment carried out with the CAPRI model. Agriculture, Ecosystems & Environment, 149, 124–134.

Yang C, Rooke JA, Cabeza I, Wallace RJ (2016). Nitrate and inhibition of ruminal methanogenesis: microbial ecology, obstacles, and opportunities for lowering methane emissions from ruminant livestock. Frontiers in Microbiology. 7:132

Zervas G and Tsiplakou E 2012. An assessment of GHG emissions from small ruminants in comparison with GHG emissions from large ruminants and monogastric livestock. Atmospheric Environment 49, 13-23.

Table 1. Potential welfare consequences of the principal strategies to mitigate greenhouse gas (GHG) emissions reported in literature.

Strategy	GHG emissions mitigation potential	Potential welfare consequences	
		Hazard	Benefit
Antimethanogens			
Chemical inhibitors	33%[1] 50%[2] 5-91%[3]	Hepatotoxic and nephrotoxic* Carcinogen*	Improved energy efficiency†
Electron receptors (Nitrates) (R)	16% [4] 27% [5] >30% [6] 17% [7]	Toxicity	Improved energy efficiency†
Ionophores (Monensin) (R)	3-5% [8] 8-9% [9] <10% [6] 27-30% [10]	Toxicity	Lower risk of acidosis Lower risk of rumen bloat Lower risk of emphysema. Improved energy efficiency†
Dietary lipids (R)	3.8% (1% fat increase)[11] 5.4% (1% fat increase)[12] 10 - 30% [6] up to 40%[13]	Too high BCS Impaired digestive function	Lower risk of NEB Improved energy efficiency†
Decrease emission intensity (Ei)			
Increase diet digestibility (A)	6.5% [14] 10-16% [15] 17% [16] 10 - 30% [6]	Too high BCS Acidosis Higher risk of bloated rumen Laminitis	Lower risk of NEB

Intensive housing (A)	8-9% (increase stocking rate in pastures) [17] 10 - 30% [6]	Higher social stress Inability to express natural behaviour Higher risk of disease spread	Lower parasite burdens
Improving health and welfare (A)	3 – 6% (by a 28 – 55% reduction of mastitis incidence in dairy cattle) [18]		Better health Extended lifespan
Increasing reproductive efficiency (A)	4% (Improving offspring survival to 80-90%) [19] 17 - 24% [20]	Higher metabolic demand Poor body condition	Higher offspring survival
Intensive breeding (A)	10 – 20% [1] 19 - 23% [2]	Impaired health traits Metabolic disorders	

BCS=Body condition score; NEB=Negative energy balance

Superscripts in each strategy refer to the species to which the strategy is likely to be applicable; "A" for all animals, "R" restricted to ruminants.

[1]Abecia *et al*., 2012; [2]Tomkins *et al*., 2009; [3]Mitsumori *et al*., 2012; [4]Van Zijderveld *et al*., 2011; [5]Hulshof *et al*., 2012; [6]Gerber *et al*., 2013; [7]Troy *et al*., 2015; [8] Beauchemin *et al*., 2010; [9]Appuhamy *et al*., 2013; [10]Guan *et al*.,2006; [11]Martin *et al*., 2010; [12]Beauchemin *et al*., 2008; [13]Machmuller, 2006; [14]Beauchemin *et al*., 2011; [15]Lovett *et al*., 2006; [16]Hales *et al*., 2012; [17]Pinares-Patino *et al*., 2007; [18]Hospido and Sonesson, 2005; [19]Beauchemin *et al*., 2011; [20]Garnsworthy, 2004.

* Hepatotoxic, nephrotoxic and carcinogen effects are hazards derived from the use of halogenated compounds but exclude the use of 3-nitrooxypropanol.

[†] Improved energy efficiency applies to all direct antimethanogenic strategies as they reduce energy loss as a result of lower methane emissions.